

Responses of leaf water potential and gas exchange to the precipitation manipulation in two shrubs on the Chinese Loess Plateau

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Abstract: Regulation of leaf gas exchange plays an important role in the survival of trees and shrubs under future climate change. However, the responses of leaf water potential and gas exchange of shrubs in semi-arid areas to the precipitation alteration are not clear. Here, we conducted a manipulated experiment with three levels of precipitation, i.e., a control with ambient precipitation, 50% above ambient precipitation (irrigation treatment), and 50% below ambient precipitation (drought treatment), with two common shrubs, *Salix psammophila* C. Wang & C. Y. Yang (isohydric plant, maintaining a constant leaf water potential by stomatal regulation) and *Caragana korshinskii* Kom. (anisohydric plant, having more variable leaf water potential), on the Chinese Loess Plateau in 2014 and 2015. We measured the seasonal variations of predawn and midday leaf water potential (Ψ_{pd} and Ψ_{md}), two parameters of gas exchange, i.e., light-saturated assimilation (A_n) and stomatal conductance (g_s), and other foliar and canopy traits. The isohydric *S. psammophila* had a similar A_n and a higher g_s than the anisohydric *C. korshinskii* under drought treatment in 2015, inconsistent with the view that photosynthetic capacity of anisohydric plants is higher than isohydric plants under severe drought. The two shrubs differently responded to precipitation manipulation. Ψ_{pd} , A_n and g_s were higher under irrigation treatment than control for *S. psammophila*, and these three variables and Ψ_{md} were significantly higher under irrigation treatment and lower under drought treatment than control for *C. korshinskii*. Leaf water potential and gas exchange responded to manipulated precipitation more strongly for *C. korshinskii* than for *S. psammophila*. However, precipitation manipulation did not alter the sensitivity of leaf gas exchange to vapor-pressure deficit and soil moisture in these two shrubs. Acclimation to long-term changes in soil moisture in these two shrubs was primarily attributed to the changes in leaf or canopy structure rather than leaf gas exchange. These findings will be useful for modeling canopy water-carbon exchange and elucidating the adaptive strategies of these two shrubs to future changes in precipitation.

Keywords: drought; irrigation; leaf water potential; gas exchange; acclimation

1 Introduction

Precipitation is one of the most important factors controlling primary productivity in terrestrial

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ecosystems (Huxman et al., 2004). Ecosystems in areas with the low mean annual precipitation are predicted to be most susceptible to projected changes of precipitation associated with climatic warming (de Dios et al., 2007). The wind-water erosion crisscross region on the Chinese Loess Plateau has the most intensive losses of soil and water in the world. Mean annual precipitation in this area is about 400 mm, but mean annual evaporation is >1500 mm (Tang et al., 1993), so water scarcity is the primary factor limiting plant growth and survival in this ecosystem. Large-scale coal and oil mining have exacerbated the shortage of water resources by depleting underground water sources, and some plants already have symptoms of dieback (Fan, 2007). Understanding the influences of projected variations of precipitation on the physiology, growth and productivity of local vegetation is therefore needed.

Plants alleviate the threat of drought in a short term by regulating stomatal closure. Therefore, plants were classified into two drought strategies based on stomatal regulation i.e., isohydry and anisohydry (Tardieu and Simonneau, 1998). Isohydric plants maintain leaf water potential (Ψ_{leaf}) by rapidly closing their stomata during drought, thus decreasing stomatal conductance (g_s) and photosynthetic assimilation. In contrast, anisohydric plants decrease Ψ_{leaf} during drought, which may increase their vulnerability to hydraulic failure. Anisohydric plants often close their stomata later, thus maintaining higher g_s and carbon assimilation under severe drought (McDowell et al., 2008). This framework has been extensively used to explain the mortality of drought-induced trees (Adams et al., 2009; Hartmann et al., 2013; Sevanto et al., 2014). Some experimental results, however, contradict this elaborate framework. For example, daily g_s decreased more for anisohydric sunflower than for isohydric maize under severe water deficit (Tardieu and Simonneau, 1998). g_s and photosynthesis were similar at the end of a dry period for co-existing isohydric and anisohydric Mediterranean woody species (Quero et al., 2011), the same pattern has been reported in different *Vitis* cultivars (Lovisolo et al., 2010). These results contradict the traditional view that anisohydric species can maintain higher levels of gas exchange under severe drought. Martínez-Vilalta and Garcia-Forner (2016) found that isohydric *Pinus edulis* exhibited chronic embolism, whereas anisohydric *Juniperus monosperma* had very little embolism, refuting the hypothesis that anisohydric species are more vulnerable than isohydric species to hydraulic failure. Garcia-Forner et al. (2016) suggested that iso/anisohydry in the regulation of Ψ_{leaf} may be independent of the dynamics of leaf gas exchange or the degree of hydraulic or carbon limitations under drought, necessitating the measurements of leaf water potential and gas exchange together rather than only inferring gas exchange or hydraulic traits from plant iso/anisohydric behavior.

The long-term acclimation of plants to limited water supply is important for their growth and survival. Experimental manipulation of precipitation has provided a way to perform controlled studies of acclimation under the long-term drought, thus improving our understanding of adaptive strategies for different plants under the projected conditions of future climate change (Weltzin et al., 2003; Huang et al., 2017). Acclimation to the long-term drought may involve the adjustment of plant morphology, physiology, anatomy, growth and/or carbon partitioning among organs. Photosynthesis is one of the most crucial physiological processes involved in acclimation (Chaves et al., 2002; Flexas et al., 2004), and the effects of the long-term drought on photosynthetic acclimation have been studied. For example, net rate of light-saturated assimilation (A_n), g_s , mesophyll conductance of CO_2 , maximum rate of carboxylation and maximum rate of electron transport all decreased when predawn Ψ_{leaf} was reduced by the manipulation of throughfall in the evergreen *Quercus ilex*, but the functional relationships between these parameters and Ψ_{leaf} were not affected by water treatments (Limousin et al., 2010). In contrast, A_n and g_s for *Q. ilex* from a mesic habitat decreased more rapidly in mesic than in dry habitats (Martin-StPaul et al., 2012). A_n under full irrigation, specific leaf hydraulic conductance and Ψ_{leaf} at zero assimilation in a mixed forest in southwestern USA decreased as precipitation decreased for both piñon and juniper trees, and leaf gas exchange acclimated to the level of precipitation in both species (Limousin et al., 2013). The long-term water stress can also invoke acclimatory responses that decrease the sensitivity of photosynthetic capacity to drought in xeric but not in riparian *Eucalyptus* species (Zhou et al., 2016). These variations in acclimatory responses suggest that functional

photosynthetic acclimation may be influenced by the climatic and soil conditions but can also vary among species/populations.

Salix psammophila C. Wang & C. Y. Yang (Salicaceae) and *Caragana korshinskii* Kom. (Fabaceae) are two typical deciduous shrubs in the wind-water erosion crisscross region on the Chinese Loess Plateau. Both shrubs play important roles in controlling soil erosion and blocking the invasion of sand. *S. psammophila* is important to the energy and paper industries, whereas *C. korshinskii* is economically important as a highly productive forage shrub. Effects of the short-term drought on seedling water relations and photosynthesis on these two species have been studied (Liu et al., 2007; Xu et al., 2012), but little is known about the responses of mature plants to the long-term drought and varied precipitation. Thus, we conducted a manipulated experiment with three levels of precipitation (a control with ambient precipitation, 50% above ambient precipitation (irrigation treatment), and 50% below ambient precipitation (drought treatment)) on these two shrubs to address the following three questions: (1) are A_n and g_s higher in *C. korshinskii* than in *S. psammophila* under severe drought due to the anisohydric behavior of *C. korshinskii* and isohydric behavior of *S. psammophila* (Li et al., 2016)? (2) does the shallow-rooted *S. psammophila* respond more strongly than *C. korshinskii* to the higher precipitation, and is it severely inhibited under drought treatment? and (3) xeric species photosynthetically acclimate to the long-term drought better than riparian species (Martin-StPaul et al., 2012; Zhou et al., 2016), so does the drought-resistant *C. korshinskii* (Ma et al., 2008; Xu et al., 2012) photosynthetically acclimate better than the drought-vulnerable *S. psammophila*?

2 Materials and methods

2.1 Study area

The study area was conducted in the Liudaogou Watershed of the Shenmu County, Shaanxi Province, China (38°46'–38°51'N, 110°21'–110°23'E; 1081.0–1273.9 m a.s.l.), which is in a typical wind and water erosion crisscross region on the Chinese Loess Plateau. The mean annual precipitation is 437 mm, with 70% falling between July and September. The annual mean temperatures is 8.4°C, with an annual accumulative temperature $\geq 10^\circ\text{C}$ of 3248°C, 153 frost-free days, total annual solar radiation of 5922 MJ/m² and mean annual sunshine duration of 2836 h (Tang et al., 1993). The area has mainly loamy, sandy and silt-dammed soils. Vegetation includes plants common in loessial and desert regions; typical woody plants are mainly trees, such as *Populus simonii* and *Salix matsudana* and shrubs, such as *S. psammophila*, *C. korshinskii*, *Amorpha fruticosa* and *Hedysarum scoparium*.

2.2 Experimental design

Two adjacent stands of healthy and uniformly growing *S. psammophila* and *C. korshinskii* on the flat top of a slope in the watershed were selected as experimental sites. Plants at the sites had been planted 30 years ago at the densities of 1600 and 2100 individuals/hm² for *S. psammophila* and *C. korshinskii*, respectively. The soil at the sites was classified as typical sandy soil. The average canopy size and height were 3.71 (± 0.14) and 3.04 (± 0.07) m for *S. psammophila* and 1.78 (± 0.08) and 2.24 (± 0.21) m for *C. korshinskii*, respectively.

The experimental design consisted of nine, randomly arranged 50 m² plots, with three replicates of three treatments per stand. The treatments were: (1) an ambient control that received a normal amount of precipitation, (2) a drought treatment with 50% less precipitation, and (3) an irrigation treatment with 50% more precipitation. We selected these lower and higher amounts of precipitation based on mean annual precipitation in the last 30 a and on the precipitation gradient (200–600 mm) within the distribution of the two shrubs on the Chinese Loess Plateau. For the drought treatment, 50% of the precipitation was diverted by transparent V-shaped troughs mounted on a steel frame at an interval of 20.0 cm. The steel frame was 2.5 m above the canopy and was supported by ten steel posts. Each post was inserted 0.5 m into the soil and fixed by concrete. The intercepted precipitation was collected and diverted by a PVC trough beside the frame and was stored in a large tank and filtered for use as the irrigation water. The

photosynthetic photon flux density at the canopy position was generally 90%–95% of that in the control, and ground-level temperature was 1°C–4°C lower during the growing season. For the irrigation treatment, water was delivered from the tank using a pump driven by a solar panel after a rainfall event with eight equally spaced sprinklers mounted about 2.5 m above the canopy. Precipitation <5 mm was not collected by the troughs, so only approximately 45% of the precipitation was diverted for application under the irrigation treatment. Vertical asbestos sheets were buried to a depth of 60 cm between plots to restrict the lateral movement of water in shallow soil. Three neutron-probe access tubes were installed to a depth of 3 m in each replicate for periodically monitoring soil moisture. The experimental setups were installed on 11 May 2014 for *C. korshinskii* and 21 May 2014 for *S. psammophila*, and no rain fell between the two installations.

Three representative plants centrally located within each plot were selected as target shrubs for measuring physiological parameters. Ψ_{leaf} , gas exchange and leaf area index (LAI) were determined for these 27 plants of each species during the growing seasons in 2014 and 2015, and foliar dry mass per unit area and foliar $\delta^{13}\text{C}$ were measured only during the growing season in 2015.

2.3 Environmental variables

Environmental variables were continuously monitored at a nearby field microclimatic station. Solar radiation (R_s) was measured using an Apogee20 PRY-P pyranometer (CS300, Apogee Instruments Inc., Logan, USA), air temperature and relative humidity (RH) were measured using a temperature and RH probe (HMP155A, Vaisala Com., Helsinki, Finland), wind speed was measured using an anemometer (Met One, Met One Instrument, Inc., OR, USA) and precipitation was measured using a tipping-bucket rain gauge (TE525MM, Texas Electronics, Texas, USA). Data were recorded on CR1000 data loggers (Campbell Scientific, Shepshed, UK) every 10 s, and averages or totals were stored every 10 min. Vapor-pressure deficit (VPD, kPa) was calculated as the difference between saturated vapor pressure (e_s) and actual vapor pressure (e_a), where e_s (Pa) was calculated using the Murray's formula (Murray, 1967):

$$e_s = 610.7 \times 10^{7.5t/(t+237.3)}, \quad (1)$$

$$e_a = \text{RH} \times e_s / 100, \quad (2)$$

where t is the temperature (°C); and RH is the relative humidity (%).

2.4 Measurements of Ψ_{leaf} and soil moisture

Predawn (Ψ_{pd}) and midday (Ψ_{md}) Ψ_{leaf} values were measured on sunny days at about 20 d intervals during the growing seasons in 2014 and 2015 using a pressure chamber (PMS 1000, PMS Instruments, Corvallis, USA). Two to three healthy mature leaves on current-year twigs from the south-facing side of each plant (6–9 leaves per plot) were measured on each measuring date. Leaves for the Ψ_{pd} and Ψ_{md} measurements were collected on the same days at 05:00–06:00 (LST, local standard time) and 12:00–14:00, respectively.

Soil moisture at a depth of 0.2–3.0 m was measured in each block at 20-cm intervals using a neutron probe (CNC 503, Beijing Chaosheng Technology Co. LTD, Beijing, China) approximately every three weeks. The neutron probe was calibrated *in situ* by saturating the ground near the experimental sites and periodically measuring soil moisture using both neutron probe and gravimetric method at different depths. The relationship between probe and gravimetric measurements was used to infer soil moisture. Soil surface (0–20 cm) moisture was measured by gravimetric method.

2.5 Measurements of gas exchange, mass per unit area and $\delta^{13}\text{C}$ of leaves

We measured two parameters of leaf gas exchange, A_n and g_s , using a portable gas exchange system (LI-6400, Li-Cor Inc., Lincoln, USA) on two mature leaves of current-year twigs from the south-facing side of three plants per block and species and on the same dates that Ψ_{leaf} was measured. A_n and g_s were measured from 09:00 to 12:00 on a sunny day, with the light source set

to a saturating photosynthetic photon flux density of 1800 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$, and ambient temperature, relative humidity and ambient CO_2 concentration were 7.4°C–27.2°C, 14.1%–62.8% and 376–402 $\mu\text{mol}/\text{mol}$, respectively, depending on the measurement date and time of the day. At the end of each measurement, the leaves enclosed in the chamber were collected for determining their projected areas that were imaged on a flatbed scanner and measured using ImageJ software (US National Institutes of Health, Bethesda, USA)

After the measurement of gas exchange, samples of leaves were pooled on 29 May and 24 August 2015 with the other mature leaves collected from current-year twigs for measuring leaf mass per unit area (LMA) and foliar $\delta^{13}\text{C}$. The leaves were oven-dried at 75°C for 48 h for determining dry mass. LMA was calculated as the ratio of dry mass to projected area. Ground dried leaves were analyzed for $\delta^{13}\text{C}$ using a continuous-flow isotope ratio mass spectrometer (DeltaPlus, Finnigan, Germany). $\delta^{13}\text{C}$ was calculated as follows:

$$\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000, \quad (3)$$

where R is the isotope ratio ($^{13}\text{C}/^{12}\text{C}$); and R_{sample} and R_{standard} are the isotope ratios of the sample and standard, respectively. The isotope values are expressed in delta notation relative to the VPDB (Vienna Pee Dee Belemnites) standard. The standard deviation for replicate analyses was $\pm 0.3\text{‰}$.

2.6 LAI

LAI was monitored for three plants in each replicated block using a LAI-2200 Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, USA). Three measurements from three directions, at intervals of 120°, were taken at half of projected canopy size between 05:30 and 08:00 on a sunny day. These measurements were taken three times in each growing season.

2.7 Data analyses

Effects of treatments on soil moisture, Ψ_{pd} , Ψ_{md} , A_n , g_s , LMA, $\delta^{13}\text{C}$ and LAI on each sampling date were tested using one-way analysis of variance (ANOVA), with individual plots as a replicate ($n=3$) for each species. A Tukey post hoc test was used to identify differences among treatments when an ANOVA identified a significant effect. The differences between species of Ψ_{pd} , Ψ_{md} , A_n and g_s for each treatment during the growing season in 2015 were detected using an independent t -test. Analysis of covariance (ANCOVA) was used to compare the regressions between g_s and A_n , between VPD and A_n or g_s , and between Ψ_{pd} and A_n or g_s among treatments for each species. We modeled the sensitivities of the gas exchange parameters to VPD and Ψ_{pd} as follows:

$$y = -m \ln \text{VPD} + n, \quad (4)$$

where m is the sensitivity of A_n or g_s to VPD; and n is the corresponding value of A_n or g_s at VPD=1 kPa (Oren et al., 1999), and

$$y = ae^{bx}, \quad (5)$$

where x is the Ψ_{pd} ; b is the sensitivity of A_n or g_s to Ψ_{pd} ; and a is the corresponding value of A_n or g_s when x is close to 0 (Zhou et al., 2016). Standard major axis was used to compare the difference of m or b between species using SMATR (Standardised Major Axis Tests and Routines) 2.0 software (Falster et al., 2006).

3 Results

3.1 Climatic variables and soil moisture

Mean annual precipitation was 439.2 mm in 2014 and 388.4 mm in 2015, and precipitation during the growing season was 373.3 mm in 2014 and 305.6 mm in 2015 (Fig. 1). When the precipitation values during the growing season and for the entire year in 2014 and 2015 were compared with the corresponding values of the multi-years (1980–2014), we found that precipitation values were almost the same as means of multi-years in 2014, but 65 mm less for the growing season and 45 mm less for the entire year in 2015, indicating that 2014 was a normal year but 2015 was a

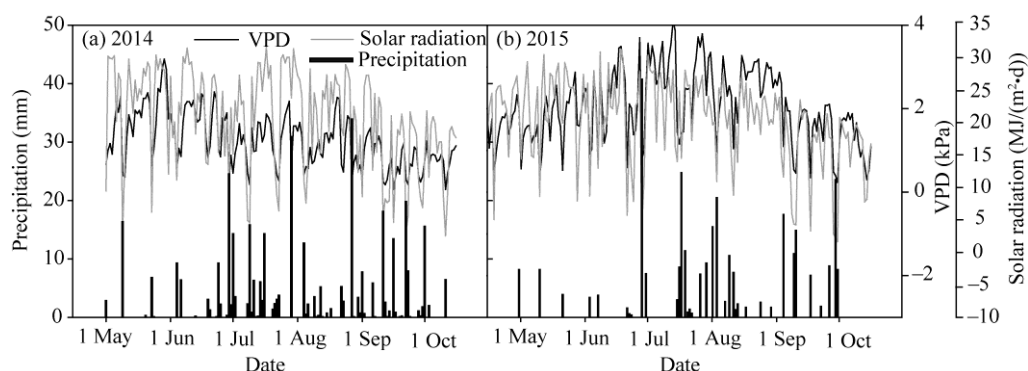


Fig. 1 Seasonal variations in precipitation, solar radiation and vapor pressure deficit (VPD) during the growing seasons in 2014 (a) and 2015 (b)

relatively dry year. Mean daytime VPD was higher in 2015 (1.46 kPa) than in 2014 (1.24 kPa), but mean daily solar radiation (20.7 MJ/(m²·d) in 2014 and 20.3 MJ/(m²·d) in 2015) did not significantly differ between the two growing seasons.

Soil moisture for all treatments was lower in 2015 than in 2014 for both species (Fig. 2), as expected. Soil moisture was relatively low under all treatments at the end of June and August in both years, corresponding to the low precipitation during these periods. The treatments did not significantly affect soil moisture at the end of June and August for both species. However, soil moisture significantly changed in the other months. Soil moisture for *S. psammophila* was generally lower under drought treatment and higher under irrigation treatment than the control during the growing season in 2014 and rainy season in 2015, no difference of soil moisture among treatments at the end of growing season in 2014 and dry season in 2015 may be related with leaf except in June–August in 2014 when soil moisture under drought treatment was not significantly decreased compared to the control. The result might be explained by the fact that the experimental setup was installed in the near term.

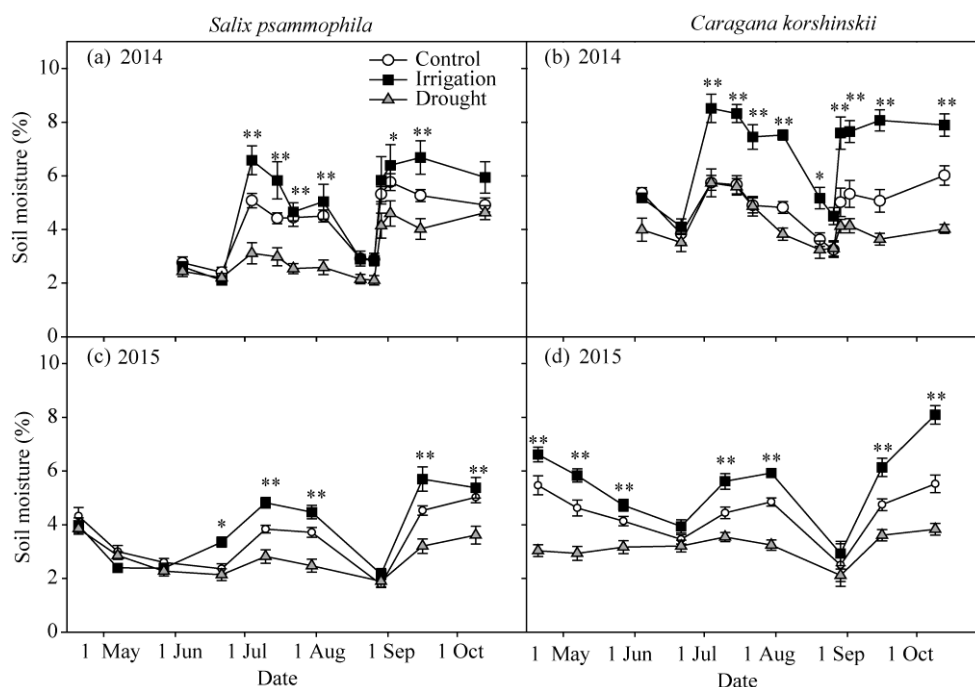


Fig. 2 Variations of soil moisture within 1.0 m soil depth for *Salix psammophila* (a and c) and *Caragana korshinskii* (b and d) under different precipitation treatments in 2014 and 2015. Bars are standard errors, $n=3$. * and ** indicate significance among three treatments at $P<0.05$ and $P<0.01$ levels, respectively.

3.2 Leaf water potential

Ψ_{pd} for *S. psammophila* during the growing seasons in 2014 and 2015 generally ranged from -0.1 to -0.5 MPa, except for at the end of June, when Ψ_{pd} was the lowest (-0.6 MPa in 2014 and -0.7 MPa in 2015, Figs. 3a and b). Ψ_{pd} for *S. psammophila* was significantly affected by the treatments on two of the nine sampling dates in 2014 ($P<0.05$; Fig. 3a) and on five of the eleven sampling dates in 2015 ($P<0.05$; Fig. 3b). Ψ_{pd} for *S. psammophila* usually responded more to irrigation than drought treatment, especially on the dates when Ψ_{pd} was significantly affected by the treatments

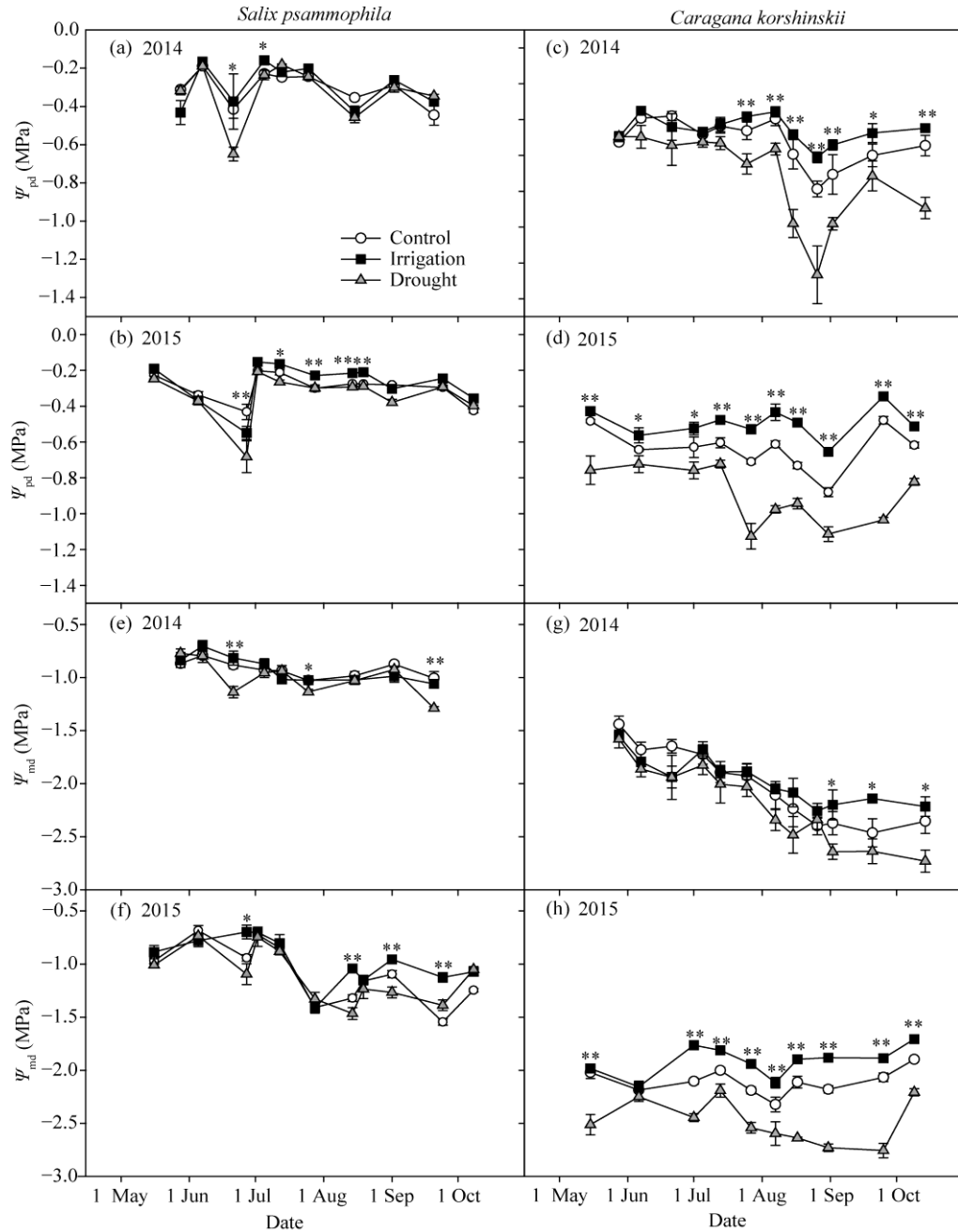


Fig. 3 Variations in predawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potentials for *Salix psammophila* (a, b, e and f) and *Caragana korshinskii* (c, d, g and h) under different precipitation treatments during the growing seasons in 2014 and 2015. Bars are standard errors, $n=3$. * and ** indicate significance among three treatments at $P<0.05$ and $P<0.01$ levels, respectively.

(Figs. 3a and b; Table 1). Ψ_{pd} for *C. korshinskii* ranged from -0.3 to -1.3 MPa during the two growing seasons, and Ψ_{pd} for *C. korshinskii* under control and irrigation treatments was relatively stable throughout the growing seasons in both years, but Ψ_{pd} under drought treatment significantly decreased during the late growing season in both years (Figs. 3c and d). Seven of the twelve Ψ_{pd} measurements in 2014 and all ten of the measurements in 2015 were significantly influenced by the treatments ($P < 0.05$). Ψ_{pd} was significantly lower under drought treatment and higher under irrigation treatment during the growing seasons in 2014 and 2015, especially on the dates when Ψ_{pd} was significantly affected by the treatments (Figs. 3c and d; Table 1).

Ψ_{md} for *S. psammophila* ranged from -0.6 to -1.6 MPa during the two growing seasons and decreased during the late growing season in 2015 (Figs. 3e and f). Three of the nine Ψ_{md} measurements in 2014 and four of the eleven measurements in 2015 were significantly affected by the treatments ($P < 0.05$). Ψ_{md} was lower under drought treatment in 2014 and higher under irrigation treatment in 2015 compared with the control on the dates when the treatments significantly affected Ψ_{md} (Figs. 3e and f; Table 1). Ψ_{md} for *C. korshinskii* ranged from -1.3 to -2.8 MPa during the two growing seasons (Figs. 3g and h). Three of the twelve Ψ_{md} measurements in 2014 were significantly affected by the treatments ($P < 0.05$). Nine of the ten Ψ_{md} measurements in 2015 were significantly affected by the treatments ($P < 0.05$), with the highest Ψ_{md} under irrigation treatment, and the lowest under drought treatment (Fig. 3h; Table 2).

Table 1 Number of days with significant treatment effects for irrigation and drought treatments when compared with the control for *Salix psammophila* and *Caragana korshinskii* during the growing seasons in 2014 and 2015

Variable	<i>Salix psammophila</i>					<i>Caragana korshinskii</i>				
	Irrigation		Drought		N	Irrigation		Drought		N
	2014	2015	2014	2015		2014	2015	2014	2015	
Ψ_{pd}	1 (+)	4 (+)	1 (-)	1 (-)	9, 11	3 (+)	9 (+)	7 (-)	10 (-)	12, 10
Ψ_{md}	0	4 (+)	3 (-)	2 (-)/2 (+)	9, 11	2 (+)	8 (+)	2 (-)	9 (-)	12, 10
A_n	0	3 (+)	1 (-)	2 (-)	8, 8	0	6 (+)	0	6 (-)	10, 8
g_s	2 (+)	3 (+)	0	1 (-)	8, 8	0	4 (+)	0	5 (-)	10, 8

Note: Ψ_{pd} and Ψ_{md} were predawn and midday leaf water potentials, respectively, A_n and g_s were light-saturated net assimilation and stomatal conductance, respectively. N was the measuring times in 2014 and 2015. The positive (+) signs indicate the increases and the negative (-) signs indicate the decreases of the number of days.

Table 2 Averaged leaf water potentials and gas exchange parameters for *Salix psammophila* and *Caragana korshinskii* during the growing season in 2015

Variable	<i>Salix psammophila</i>			<i>Caragana korshinskii</i>		
	Control	Irrigation	Drought	Control	Irrigation	Drought
Ψ_{pd} (MPa)	-0.30	-0.27 (10.00)	-0.34 (-13.33)	-0.65*	-0.50 (23.08)*	-0.91 (-40.00)*
Ψ_{md} (MPa)	-1.09	-0.97 (11.01)	-1.09 (0.00)	-2.11*	-1.93 (8.53)*	-2.51 (-18.96)*
A_n ($\mu\text{mol}/(\text{m}^2\cdot\text{s})$)	13.85	16.71 (20.65)	12.16 (-12.20)	16.24*	21.66 (33.37)*	11.33 (-30.23) ^{ns}
g_s ($\text{mmol}/(\text{m}^2\cdot\text{s})$)	119.00	142.50 (19.80)	106.10 (-10.85)	116.00 ^{ns}	159.20 (37.25)*	75.80 (-34.66)*

Note: Ψ_{pd} and Ψ_{md} were predawn and midday leaf water potentials, respectively, and were measured for 11 times in *Salix psammophila* and 10 times in *Caragana korshinskii*. A_n and g_s were light-saturated net assimilation and stomatal conductance, respectively and were measured 8 times for both species. The numbers within parentheses are the percentage increase relative to the control value, with positive value indicating increase and negative value indicating decrease. * and ^{ns} indicate significance between two species at $P < 0.05$ and $P > 0.05$ levels, respectively.

Ψ_{pd} and Ψ_{md} were generally lower for *C. korshinskii* than for *S. psammophila* in both years (Fig. 3; Table 2). There was no significant correlation between Ψ_{pd} and Ψ_{md} for *S. psammophila* (Fig. 4a), but Ψ_{pd} was positively correlated with the water potential gradient ($\Delta\Psi$, $\Psi_{pd} - \Psi_{md}$, $P < 0.05$; Fig. 4b). Ψ_{pd} was positively correlated with Ψ_{md} for *C. korshinskii* ($P < 0.05$; Fig. 4c), but Ψ_{pd} was not significantly correlated with the water potential gradient (Fig. 4d).

3.3 Leaf gas exchange

Parameters of leaf gas exchange for *S. psammophila* seasonally fluctuated, with A_n and g_s much

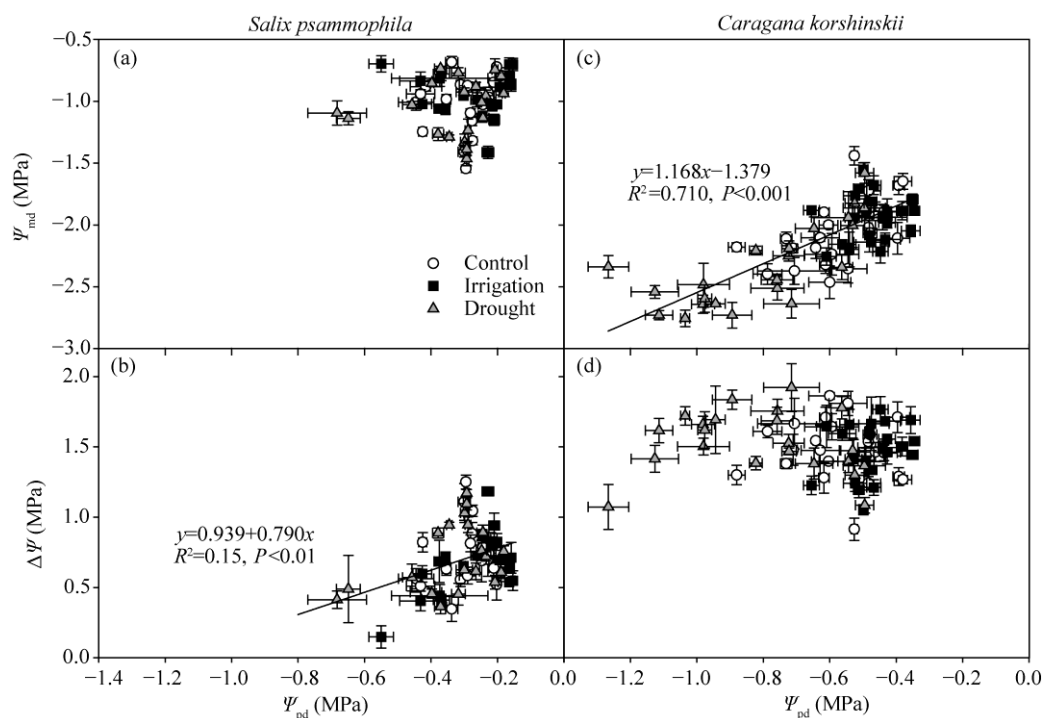


Fig. 4 Relationships of predawn leaf water potential (Ψ_{pd}) with midday leaf water potential (Ψ_{md}) and water potential gradient ($\Delta\Psi$, $\Psi_{pd} - \Psi_{md}$) for *Salix psammophila* (a and b) and *Caragana korshinskii* (c and d) under different precipitation treatments. Bars are standard errors. Data from 2014 and 2015 were pooled together, in which $n=9$ in 2014 and 11 in 2015 for *S. psammophila*, and 12 in 2014 and 10 in 2015 for *C. korshinskii*.

lower at the end of June and in mid-to-late August during the two growing seasons (Fig. 5). These decreases corresponded to the lower precipitation and soil moisture during these periods (Figs. 1 and 2). Only one A_n and two g_s of the eight measurements of leaf gas exchange for *S. psammophila* in 2014 were significantly affected by the treatments ($P < 0.05$; Figs. 5a and b). Four A_n and three g_s of the eight measurements in 2015 were significantly affected by the treatments ($P < 0.05$; Figs. 5c and d). A_n and g_s responded more to the irrigation treatment on the sampling dates when the treatment had significant effects (Figs. 5a and d; Tables 1 and 2). A_n for *C. korshinskii* peaked in mid-to-late August during the two growing seasons. Treatments did not significantly affect A_n or g_s in 2014 (Figs. 5e and f). All eight A_n and g_s measurements were significantly affected by the treatments in 2015 ($P < 0.05$), with the highest A_n and g_s values under irrigation treatment, followed by the control and the lowest under drought treatment (Figs. 5g and h; Tables 1 and 2).

A_n and g_s for both species responded to precipitation manipulation more in 2015 than in 2014 (Fig. 5). A_n and g_s during the growing season in 2015 were higher for *C. korshinskii* than for *S. psammophila* under irrigation treatment, but A_n was similar and g_s was even lower than that of *S. psammophila* under drought treatment (Table 2), indicating that *C. korshinskii* did not have a higher photosynthetic capacity than *S. psammophila* under severe drought. The response pattern and magnitude of A_n and g_s to precipitation manipulation differed between the two species. A_n and g_s for *S. psammophila* clearly responded to irrigation but seldom to drought treatment. In contrast, A_n and g_s for *C. korshinskii* responded strongly to both irrigation and drought treatments relative to the control (Tables 1 and 2). The response magnitude of both irrigation and drought treatments was larger for *C. korshinskii* than for *S. psammophila* (Table 2). Precipitation treatments did not affect the linear relationship between A_n and g_s for these two species (Fig. 6).

3.4 Sensitivities of leaf gas exchange to VPD and Ψ_{pd}

Treatment and VPD or Ψ_{pd} did not significantly interact with A_n and g_s for either species ($P > 0.05$)

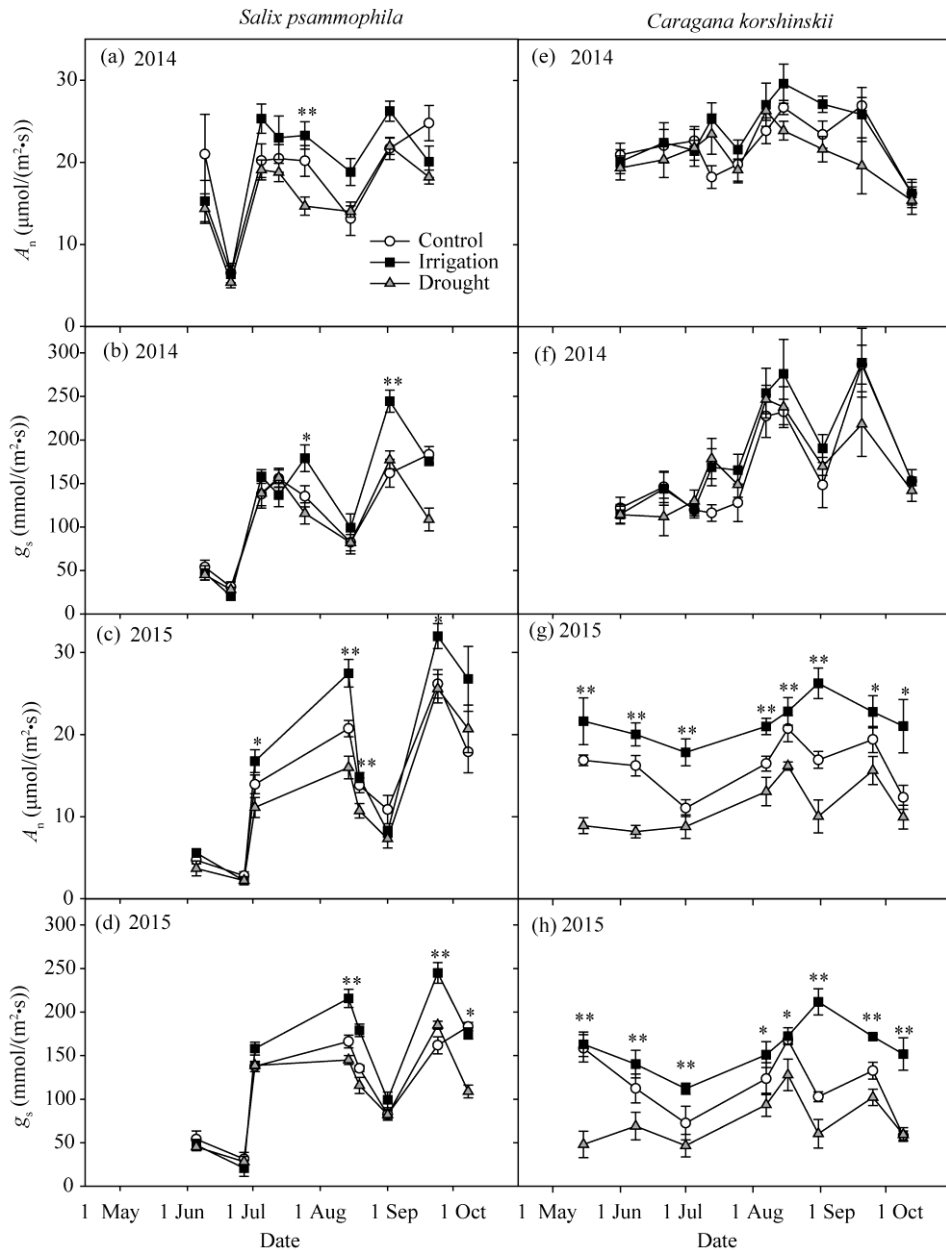


Fig. 5 Variations in light-saturated net assimilation (A_n) and stomatal conductance (g_s) for *Salix psammophila* (a, b, c and d) and *Caragana korshinskii* (e, f, g and h) under different precipitation treatments during the growing seasons in 2014 and 2015. Bars are standard errors, $n=3$. * and ** indicate significance among three treatments at $P<0.05$ and $P<0.01$ levels, respectively.

in the ANCOVA, so the relationships between A_n and VPD or Ψ_{pd} , g_s and VPD or Ψ_{pd} did not differ among the treatments. When we pooled together the data from all treatments, leaf gas exchange decreased with increasing VPD and Ψ_{pd} , and decreased faster for *S. psammophila* than for *C. korshinskii* ($P<0.05$; Figs. 7 and 8), indicating a higher sensitivity of gas exchange to VPD and Ψ_{pd} . A_n and g_s were the highest at $\Psi_{pd} = -0.2$ MPa for *S. psammophila* and at $\Psi_{pd} = -0.4$ MPa for *C. korshinskii*. Ψ_{pd} at a 50% loss of maximum A_n was -0.39 MPa for *S. psammophila* and -1.25 MPa for *C. korshinskii*, with a corresponding Ψ_{pd} at a 50% loss of maximum g_s of -0.42 MPa for *S. psammophila* and -1.21 MPa for *C. korshinskii*. Ψ_{pd} corresponding to 50% losses of maximum A_n and g_s was lower for *C. korshinskii* than for *S. psammophila*, suggesting that the

photosynthetic apparatus was more resistant to drought for *C. korshinskii* than for *S. psammophila*.

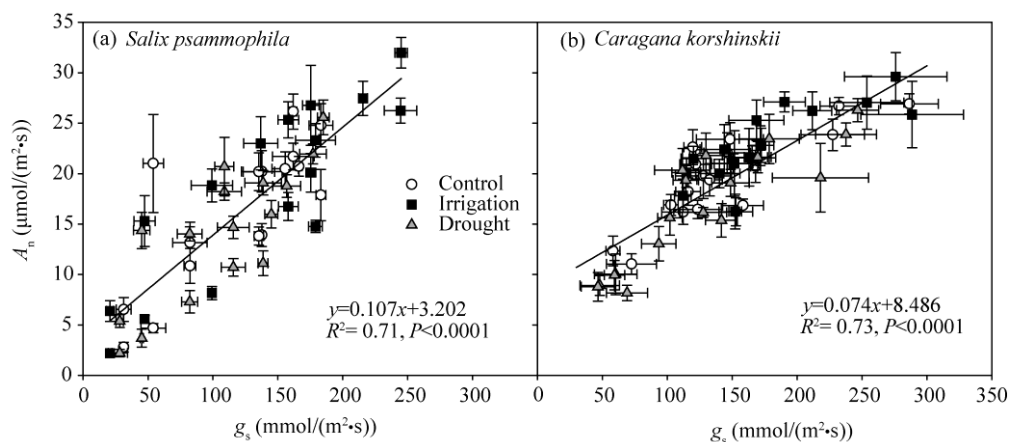


Fig. 6 Relationship between light-saturated net assimilation (A_n) and stomatal conductance (g_s) for *Salix psammophila* (a) and *Caragana korshinskii* (b) under different precipitation treatments. Bars are standard errors. Data from 2014 and 2015 were pooled together, in which $n=48$ for *S. psammophila* and 54 for *C. korshinskii*.

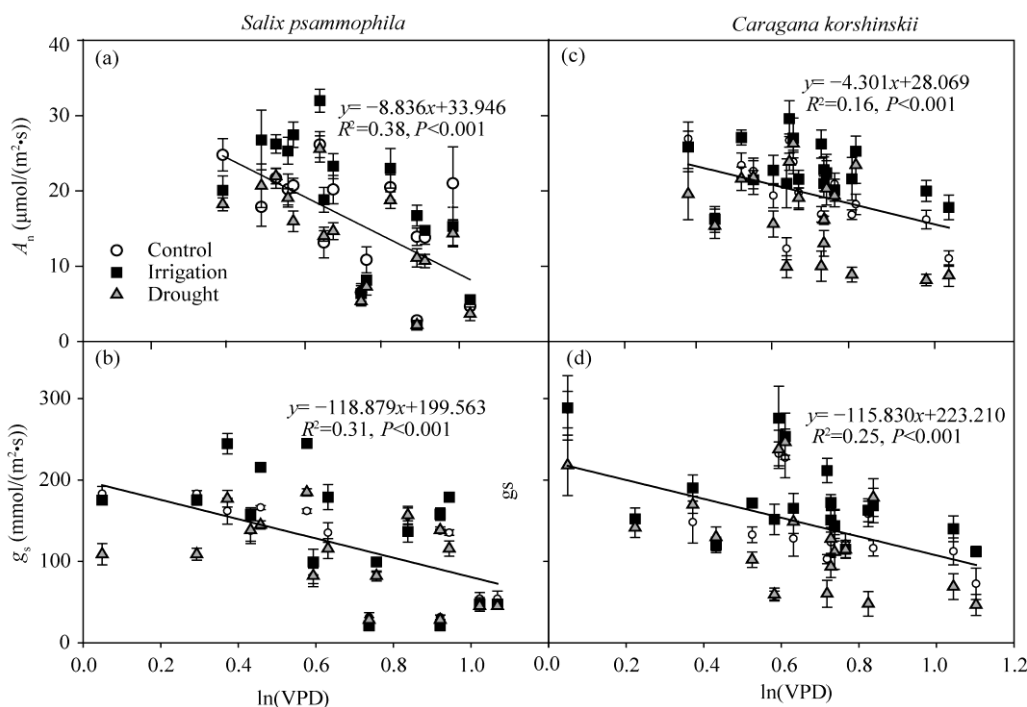


Fig. 7 Relationships of light-saturated net assimilation (A_n) and stomatal conductance (g_s) with VPD (vapor pressure deficit) for *Salix psammophila* (a and b) and *Caragana korshinskii* (c and d) under different precipitation treatments. Bars are standard errors. Data from 2014 and 2015 were pooled together, in which $n=48$ for *S. psammophila* and $n=54$ for *C. korshinskii*.

3.5 LMA, $\delta^{13}\text{C}$ and canopy LAI

Leaf $\delta^{13}\text{C}$ and LMA for *S. psammophila* during the growing season in 2015 were significantly affected by the treatments ($P<0.05$), with $\delta^{13}\text{C}$ and LMA lower under irrigation treatment than the control. Treatments, however, did not significantly affect $\delta^{13}\text{C}$ or LMA for *C. korshinskii* (Table 3). Drought significantly decreased LAI for *S. psammophila* in 2015 and for *C. korshinskii* in both two seasons, and irrigation increased LAI for *C. korshinskii* during the middle growing season in 2015 (Fig. 9).

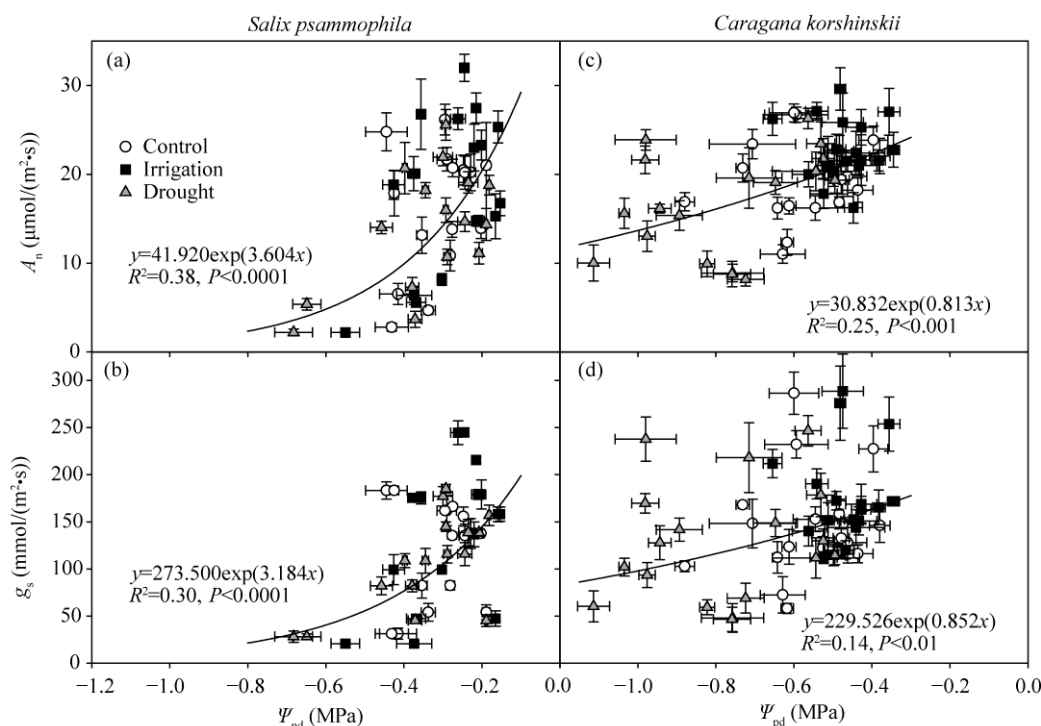


Fig. 8 Relationships of light-saturated net assimilation (A_n) and stomatal conductance (g_s) with predawn leaf water potential (Ψ_{pd}) for *Salix psammophila* (a and b) and *Caragana korshinskii* (c and d) under different precipitation treatments. Bars are standard errors. Data from 2014 and 2015 were pooled together, in which $n=48$ for *S. psammophila* and $n=54$ for *C. korshinskii*.

Table 3 Leaf mass per area (LMA) and $\delta^{13}\text{C}$ for *Salix psammophila* and *Caragana korshinskii* during the growing season in 2015

Species	Treatment	LMA (g/m ²)		$\delta^{13}\text{C}$ (‰)	
		May	August	May	August
<i>Salix psammophila</i>	Control	74.33±2.03 ^a	123.05±5.40 ^a	-24.8±0.1 ^a	-25.6±0.2 ^{ab}
	Irrigation	61.11±3.37 ^b	99.11±9.85 ^b	-25.4±0.1 ^b	-26.0±0.1 ^b
	Drought	72.00±2.08 ^a	125.09±10.7 ^a	-25.0±0.3 ^{ab}	-25.2±0.1 ^a
<i>Caragana korshinskii</i>	Control	63.37±1.68	104.30±2.79	-25.2±0.1	-26.2±0.4
	Irrigation	61.77±2.92	104.73±1.37	-25.5±0.4	-25.7±0.3
	Drought	59.42±1.23	89.92±3.48	-24.9±0.2	-25.9±0.1

Note: Mean±SE, $n=3$. Different lowercase letters indicate significance among different treatments at $P<0.05$ level.

4 Discussion

4.1 Strategies of stomatal regulation and carbon assimilation in two shrubs

S. psammophila is an isohydric plant, whereas *C. korshinskii* is an anisohydric plant, based on seasonal changes in Ψ_{leaf} , daily stomatal regulatory capacity and stem hydraulic vulnerability (Dong and Zhang, 2001; Jiang and Zhu, 2001; Xu et al., 2012; Li et al., 2016). Seasonal fluctuations in Ψ_{pd} and Ψ_{md} for *S. psammophila* were small, and Ψ_{pd} and Ψ_{md} were not significantly affected by drought and correlated for most sampling dates (Fig. 3). Ψ_{pd} and water potential gradient were significantly correlated, suggesting that *S. psammophila* could maintain Ψ_{pd} and adjusted its water potential gradient when soil water potential decreased, behaving as a typical isohydric plant (Tardieu and Simonneau, 1998; Martínez-Vilalta and García-Forner, 2016). In contrast, seasonal fluctuations in Ψ_{pd} and Ψ_{md} and the effects of drought

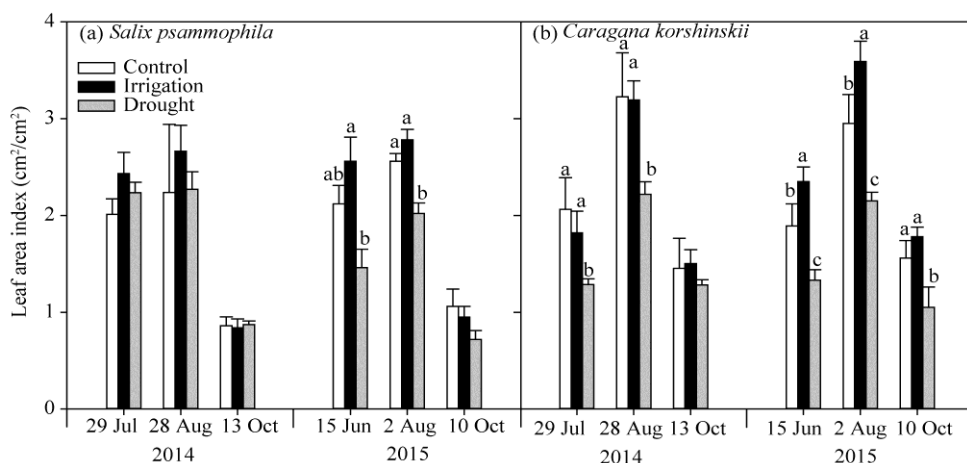


Fig. 9 Leaf area index of *Salix psammophila* (a) and *Caragana korshinskii* (b) under different precipitation treatments during the growing seasons in 2014 and 2015. Bars are standard errors, $n=3$. Different lowercase letters indicate significant differences among different treatments at $P<0.05$ level.

on Ψ_{pd} and Ψ_{md} were larger for *C. korshinskii* than for *S. psammophila* (Fig. 2). The linear regression between Ψ_{pd} and Ψ_{md} was significant, but Ψ_{pd} was not significantly correlated with the water potential gradient for *C. korshinskii*, suggesting that Ψ_{md} decreased as soil water potential decreased and that this shrub behaved as an anisohydric plant (Tardieu and Simonneau, 1998; Martínez-Vilalta and García-Forner, 2016).

A_n and g_s were higher for *C. korshinskii* than for *S. psammophila* under irrigation treatment, perhaps due to the higher leaf N content (1.84% for *C. korshinskii* and 1.05% for *S. psammophila*) of this leguminous species. A_n was similar for *C. korshinskii* and *S. psammophila*, and g_s was lower for *C. korshinskii* than for *S. psammophila* under severe drought (Table 2), inconsistent with the higher A_n and g_s for anisohydric than for isohydric plants under extreme drought. This pattern has been reported for various crops, woody species and *Vitis* cultivars (Tardieu and Simonneau, 1998; Lovisolo et al., 2010; Quero et al., 2011), further suggesting that iso/anisohydric behavior based on the regulation of Ψ_{leaf} may be difficult to associate with their gas exchange behavior (Martínez-Vilalta and García-Forner, 2016).

4.2 Responses of Ψ_{leaf} and gas exchange to precipitation manipulation

The parameters of Ψ_{leaf} and gas exchange for both shrubs responded to the precipitation manipulation, but the patterns of response differed between the two species. The response of *S. psammophila* to irrigation and drought treatments was asymmetrical. Ψ_{pd} , A_n and g_s for *S. psammophila* were higher under irrigation treatment than under the control but were similar between drought and control treatments. Ψ_{pd} , Ψ_{md} , A_n and g_s for *C. korshinskii* all responded symmetrically to irrigation and drought treatments. All these variables were higher under irrigation treatment and lower under drought treatment than under the control (Figs. 3 and 5; Tables 1 and 2). These different patterns of response between the two shrubs may be due to the hydraulic constraints, especially root distribution and the acclimation of water uptake by roots.

S. psammophila has shallow roots, with roots not exceeding 1.5 m, but the roots spread horizontally by up to 3-fold of the canopy size. This root configuration restricts *S. psammophila* to water supplies in shallow soil (Liu et al., 2010), so Ψ_{leaf} and gas exchange for this species are very sensitive to irrigation. Stronger stomatal regulation in the isohydric *S. psammophila* may have limited responses of Ψ_{leaf} , A_n and g_s to drought on most of the measuring dates. *C. korshinskii* has a taproot system with dense lateral roots, and roots can reach deeper than 6.0 m for 12–15-year-old plants (Niu et al., 2003). A hydrogen isotope experiment in the Ulanbuh Desert found that *C. korshinskii* mainly acquired water from depths of 0–30 and 60–90 cm during late autumn (Zhu et al., 2010), suggesting that its root system took up water from both shallow and deep layers. This versatile strategy for acquiring water likely accounts for the symmetrical patterns of the responses of Ψ_{leaf} , A_n and g_s to irrigation and drought treatments. The asymmetrical pattern of response of *S. psammophila* to the water treatments in our study was similar to the

pattern in the isohydric *P. edulis* in southwestern USA, whereas the symmetrical patterns for *C. korshinskii* differed from that for anisohydric *J. monosperma* (Limousin et al., 2013). The photosynthetic capacity of *J. monosperma* was similar in irrigation and control plots and was significantly lower under drought treatment (Limousin et al., 2013). These differences in response to precipitation manipulation between two anisohydric species may be due to a greater reliance on deep soil water in *J. monosperma* than in *C. korshinskii*.

C. korshinskii responded more strongly than *S. psammophila* to the precipitation manipulation, outperformed *S. psammophila* under irrigation treatment and was severely inhibited under drought treatment (Table 2). Leaf N content was higher for *C. korshinskii* than for *S. psammophila* due to its function of fixing N, which may help to increase photosynthetic capacity under irrigation in the nutrient-limited area. The high infiltration capacity of the sandy soils at the sites may also have allowed rainwater to quickly infiltrate to deep soil, which would be difficult to access by the shallow-rooted *S. psammophila*. Our previous data for the growth of these two shrubs (Ai et al., 2017) also demonstrated that seasonal increase in aboveground biomass was larger for *C. korshinskii* than for *S. psammophila* under irrigation treatment but smaller under drought treatment, supporting the validity of our data for gas exchange. The greater plasticity of Ψ_{leaf} and gas exchange for *C. korshinskii* may increase its fitness in highly variable environments, partly contributing to the wide distribution of this species on the Chinese Loess Plateau. The stricter stomatal regulation and more conservative response of gas exchange to drought for *S. psammophila*, however, may increase its adaptation in drought and desert areas, so the two shrubs may have different strategies for adapting to a long-term drought.

4.3 Acclimation of leaf gas exchange to the long-term alteration of water supply

The sensitivities of leaf A_n and g_s to VPD or Ψ_{pd} did not differ among the treatments for either species, suggesting that VPD and precipitation manipulation did not alter the functional relationship between leaf gas exchange and water stress. These findings are consistent with those reported for the evergreen trees *Q. ilex* and *Arbutus unedo* in a Mediterranean Macchia ecosystem (Nogués and Alegre, 2002; Ripullone et al., 2009; Limousin et al., 2010; Mission et al., 2010), suggesting that two years of variation in soil moisture did not acclimate photosynthetic gas exchange in the plants. Studies of *Q. ilex* across a precipitation gradient (Martin-StPaul et al., 2012), piñon and juniper trees under precipitation manipulation in southwestern USA (Limousin et al., 2013) and xeric *Eucalyptus* species (Zhou et al., 2016), however, have reported acclimatory responses in the sensitivity of photosynthetic capacity to a long-term drought. These contradictions among studies may be due to the differences in species, developmental stage (seedling, sapling and mature tree) and degree of water stress.

Long-term structural adjustment may alleviate the effects of drought on photosynthesis and g_s (Maseda and Fernández, 2006). The treatments of precipitation manipulation influenced LMA for *S. psammophila*, which was lower under irrigation treatment. The higher photosynthetic rate and lower integrated water-use efficiency (lower foliar $\delta^{13}\text{C}$) for *S. psammophila* under irrigation treatment than under the control may therefore be partly attributed to the changes in foliar structural properties. Leaves with a lower LMA generally have higher rates of A_n and lower water-use efficiencies (Lamont et al., 2002; Gullías et al., 2003). LMA for *C. korshinskii* was not significantly influenced by the treatments, so the responses of leaf gas exchange to the irrigation and drought treatments were likely due to factors other than the alteration of foliar structure. LAI was significantly lower under drought treatment than under the control for both shrubs and was partly higher under irrigation treatment in 2015 (Fig. 8), indicating an acclimatory response of canopy structure. Changes to hydraulic conductance in soil-plant systems may be responsible for altered leaf gas exchange in precipitation manipulation (Ripullone et al., 2007; Limousin et al., 2013; Zhou et al., 2016), so foliar and canopy properties may serve as potential regulators of water uptake by roots and hydraulic transport, possibly affecting photosynthesis in these two shrubs.

Finally, this study identified the behavior of mature shrubs in a natural environment in response to projected variation in precipitation, but our experiments were conducted only for two years. Long-term experiments are thus needed to characterize the drought resistance and resilience of these fragile ecosystems to projected climate change.

5 Conclusions

Two consecutive years of precipitation manipulation did not alter the strategy of stomatal control in the two shrubs. A_n was similar for isohydric *S. psammophila* and anisohydric *C. korshinskii*, and g_s was even higher for *S. psammophila* under severe drought, inconsistent with the view that A_n and g_s under extreme drought are higher for anisohydric plants. Parameters of Ψ_{leaf} and gas exchange (Ψ_{pd} , Ψ_{md} , A_n and g_s) for *S. psammophila* were most strongly influenced by irrigation treatment and for *C. korshinskii* were significantly influenced by both irrigation and drought treatments. Ψ_{leaf} and gas exchange were more plastic to irrigation and drought treatments for *C. korshinskii*. Precipitation manipulation did not alter the sensitivity of leaf gas exchange to VPD or soil moisture in either species. Acclimation to changes in soil moisture for the two species was primarily due to the changes in foliar structure (e.g., LMA) and/or canopy structure (e.g., LAI) rather than photosynthetic gas exchange. These findings may be useful for modeling water-carbon exchange in canopy and elucidating the adaptive strategies of these two shrubs to future changes in precipitation.

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